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Introducing entomophagous insects to control pests: prediction of target species density

Интродукция насекомых-энтомофагов против вредителей: прогнозирование плотности популяции вида-мишени в случае интродукции насекомых

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ABSTRACT. It is second attempt prediction results of classical biological control. We retrospective assesed the perspective of the introduction of two species of parasites (*Blepharipoda scutellata* R.-D. and *Parasetigena silvestris* R.-D.) against *Lymantria dispar* L. The difference between predicted level of steady-state density of the host population and reality due to big errors estimated parameters (both for the parasites and the host). If for best investigated case the prediction is very approximate any assertion about absent perspective introduction parasites predators and competitor is false.

РЕЗЮМЕ. Представлена попытка прогнозирования результатов классического биологического контроля. Учитывая опыт прошлого, мы оценивали перспективу интродукции двух видов тахин (*Blepharipoda scutellata*R.-D. и*Parasetigena silvestris* R.-D.) против *Lymantria dispar* L. Разница между прогнозируемым результатом уровня стабилизации (особая точка) популяции хозяина и действительностью, обусловлена большими погрешностями оцениваемых параметров (как для популяции паразита, так и для популяции хозяина). Несмотря на то, что в данном случае имеется относительно богатая информация, результат все-таки получается очень приблизительным. Таким образом, всегда любое утверждение относительно отсутствия перспектив интродукции энтомофагов является ненадежным.

Introduction

Since the first half of the 20-th century introductions of predator and parasitoid insects aimed at pest control were widely applied. The primery impulse was made by large-scale introduction projects carried out in the USA and Canada mainly to control gypsy moth and brown-tail moth [Howard and Fiske, 1911; Mc Gugan and Coppel, 1962]. Later on this methodology was used (with no 100 % success) in controlling numerous agricultural and forest pests. Success has been reached in 16% and partially in 58% of the cases [Hall et al., 1980].

It should be mentioned that the methodology came to practice prior to be properly justified, since the theory had not been adequately developed. Perhaps, only a part of it considered the issues climatic suitability [Coppel and Mertins,1977; Izhevsky,1990]was advanced. As for the biological basis of selecting parasitoid species for introduction, it has always been biased. In special literature one can find a list of requirments that introduced species should meet [Coppel, Mertins, 1977; Hall et al., 1980; Huffaker, Messenger, 1976; Izhevsky, 1990]. However, in practice low data quality or lack of information on some particular mechanisms of the introduction process did not slow down introductions. This approach was promoted, for instance, by Huffaker et al. [1971]. They wrote, in particular, that there is no need to study parasites and predators before introduction, since it is almost impossible to predict the effect of introduction. They proposed to introduce many parasitoid species so as to find out the best one. Probably, such an approach (supported to a certain extent by the majority of specialists) along with the improperly planned and made experiments as well as lack of detailed observations on parasites and predators, provided relatively low success of the introduction projects.

There is huge number of population dynamics models for insects (literarute is not cited). However, any complete analysis of the introduction through even some promising models (see reviews Sharov, 1986; May, 1976) has not yet been accomplished. No evaluation of the behavior of the models under conditions similar to the natural ones was done [Varley, 1974; Hassell, Varley, 1973]. We think that the main reason of this abnor-

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mal situation is lack of publications on detailed biological observations (presented in numerical form) as well as low quality of some biological research.

Computerised expert systems are powerful tool for the forecast of results of classical biological control. Expert system is simply an instrument. It is a good tool if it is comfortable to use and using it gives good results. Such systems are useful for the education and the practical biological control. Prognosis is based on the retrospection analysis experience classical biological control and the modern theory of dynamics of population density.

But mathematical approach is typically not use in practical biological control programs. Perhaps because of many entomologists are lacking in higher level mathematical knowledge.

However, all the above does not mean that mathematical approach to the problem is impossible. Careful and critical review of published data as well as additional detailed observations on the majority of well-known pests and parasitoids can help provide valuable predictions using models.

Methods

Example of mathematical analysis of the introduction

Just to illuminate an approach to prediction of the results of introduction we chose gypsy moth (*Lymantria dispar L.*) — one of the well-studied pests. Since detailed information on parasites and predators dynamics is needed to develop a model, we chose only two species parasitoids on which data were published in periodicals: 1) *Blepharipoda scutellata* R.-D. (*=Sturmia scutellata* R.-D., *=Blepharipa scutellata* R.-D., *=B. pratensis* Meig., *=Blepharipoda pratensis* Meig., *=Herigia pratensis* Meig.) (Diptera: Tachinidae); 2) *Parasetigena sylvestris* R.-D. (*=Phorocera silvestris* R.-D., *=Ph. agilis* R.-D., *=Ph. segregata* Rond.) (Diptera: Tachinidae). Both species are solitary internal parasites of half-grown and larger gypsy moth caterpillars. Gypsy moth are the most preferable host for them [Zerova et al., 1989]. Both species have been introduced to the USA and well established there [Clausen, 1956].

Three data sets (7, 11 and 14 year time series) on the host and both parasitoids referred to the native area were extracted from publications [Znamenski, Lyamtcev, 1990; Panina, 1985; Lyamtcev, 1985; Sisojevic, 1975; Yafaeva, 1963]. These data were used as a basis for modeling. The authors mentioned above have used different units for the estimates of the population density: number per 100 cluster of leafs [Znamenski, Lyamtcev, 1990; Panina, 1985; Lyamtcev, 1985], number per tree [Lyamtcev, 1985; Yafaeva, 1963], number per 100 m^2 [Sisojevic, 1975]. All data were converted into number of individuals per 100 m^2. The conversion was made using the methods proposed by Lyamtcev [1985] and regional tables of forest growth [Growth of the main ..., 1967].

Thus, we have only three rather short time series. Therefore, we need to simplify model structure as much as possible. The following assumption were used while constructing the model:

1. Populations of host and parasites are local (neither emigration nor immigration are supposed).
2. Both parasitoids act independently (i. e., probability of not getting attacked by both parasites is product of respective figures referred calculated for an each parasite separately).
3. All hosts are accessible for both parasitoids (no shelters exist).
4. Parasitoids emerge from all the hosts attacked; mortality of parasitoids at the span "larvae in host — imago" is constant.

As a basis of the model we use logistic equation discribing host-parasite interactions by Nicholson and Bailey [1935] and Hassell and Varley [1969]. The model parameters were estimated using SYSTAT (version 4.1).

The following equation shows how host population density N_{n+1} at the next generation depends on its density N_n at the current one:

$$N_{n+1}=N_n*R*(1-N_n/K)*EXP(-Q_{bl}*P_{bl,n}^{1-m1})*EXP(-Q_{pp}*P_{pp,n}^{1-m2}) \quad (1),$$

where R — fundamental net reproductive rate the host population, K — upper limit host population density, $P_{bl,n}$ — density of searching imago of *B.scutellata* of the current generation (number per 100 m^2), $P_{pp,n}$ — density of searching imago of *P. silvestris* of the current generation (number per 100 m^2), Q_{bl} — quest constant for *B. scutellata*, m_1 — mutual interference constant for *B. scutellata*, Q_{pp} — quest constant for *P. silvestris*, m_2 — mutual interference constant for *P. silvestris*.

It is also assumed that

$$P1 = N0*EGG*0.5*WBL*S1 \quad (2),$$

$$P2 = N0*EGG*0.5*WPP*S2 \quad (3),$$

where N0*EGG*0.5 is number of half-grown gypsy moth caterpillars accessible for the parasites in previous generation; 0.5 is survival of hosts at the stages egg-larvae of the 2-nd instar; W_{bl}, W_{pp} proportion of hosts infected by *B. scutellata* and *P. silvestris* in previous generation, respectively; P1 and P2 post hunting density of populations of *B. scutellata* and *P. silvestris,* respectively.

Lack of accurate data did not allow us to use variable EGG (mean number of eggs in the eggmasses in spring of the previous year). It was replaced by constant, namely by 350 (mean number of eggs in eggmasses).

The constants S1 and S2 were calculated as follows: S1=0.45*0.5; S2=0.4*0.5, where 0.45 is survival of *B. scutellata* at the period "larvae in host — imago" (the estimates given by Sisojevic [1975] and Zerova et al. [1989], were averaged); 0.4 is survival of *P. silvestris* at the period "larvae in host — imago" (the estimates given by Sisojevic [1975] and Zerova et al. [1989], were averaged); 0.5 is proportion of females in parasitoid populations (actual data is not available).

Dynamics of parasite populations was modeled as follows:

$$P_{blN+1}=N_n*S1*(1-EXP(-Q_{bl}*P_{bl}^{1-m1}))*EXP(-Q_{pp}*P_{pp}^{1-m2}) \quad (4)$$

$$P_{ppN+1}=N_n*S2*(1-EXP(-Q_{bl}*P_{pp}^{1-m2}))*EXP(-Q_{bl}*P_{pp}^{1-m1}) \quad (5),$$

where P_{blN+1}, P_{ppN+1} — density of searching parasitoides of *B. scutellata* and *P. silvestris* of the next generaion, respectively.

According to Hassell and Varley [1969]:

$$QP^{1-m}=Ln\frac{N_n}{N_n - W*N_n} \quad (6),$$

where N_n — host population density at n-th generation, $N_n - W*N_n$ — density of hosts remained uninfected, W — proportion of hosts infected by both parasites.

The estimation yielded the following values:

B. scutellata: Q_{bl}=0.213±0.022, m1=0.895±0.016,

P. silvestris: Q_{pp}=0.048±0.032, m2=0.596±0.116.

Net fundamental reproductive rate (R) = 1.28

For the USA the data on the US populations was extracted from the article of Campbell [1967].

The role of the introduced parasites in 1910-1921 was considered as insignificant.

The analysis of population dynamics of gypsy moth before introduction of parasites and predators was made using logistic model: $N_{n+1}=N_n*R*(1-N_n/K)$ (7),

where R= 1.580±0.408 and K= 347.704±66.

Results

Prediction of the results of introduction was made on the basis of model (1).

We assumed that the searching ability of parasites (expressed by Q and m) did not change during the introduction.

For mean case, forecasted mortality caused*B. scutellata* and *P. silvestris* was 33% and 5%, respectively. Ferguson et al. [1994] reported mortality 32%, and 26%, respectively. Mortality due this species is 24% and 27%, respectivily in homeland.

The model runs simulating introduction showed sustainable increase of parasitoid population densities after temporary gradual decrease. Usually they also showed that host population density declined while reaching stability (N*). Temporary increase of host population density may occur at the beginning of the process, especially if the magnitude of R is comparatively high. Oscillations of parasitoid population density occur only in some cases, for instance if m>1. The results of the simulation are presented at Table 1 and Fig.1.

While running the model, the following ranges of parameters were investigated. As lower limits of Q, m (Fig.1) the minimum possible values (mean value minus error) were used; the only exception was made for Q_{pp} which lower limit was 0.001. The upper limits of the ranges were maximum possible values (mean value plus error). The ranges were devided into 10 (for Q and Q, m) and into 20 (for m and R). The runs were terminated when the difference between the current and subsequent values of the host density had become less than 0.0001. It usually took less than 50 iterations.

The difference between levels of steady-state density of the host population can be of four orders due to big errors in the estimated parameters (both for the parasites and the host).

Discussion

We know one attemt of prediction result of introduction parasites [Varley, Gradvell, 1968].

The result of introduction is remarkable similar to the prediction for biological control in Canada made by Varley and Gradvell in 1968.

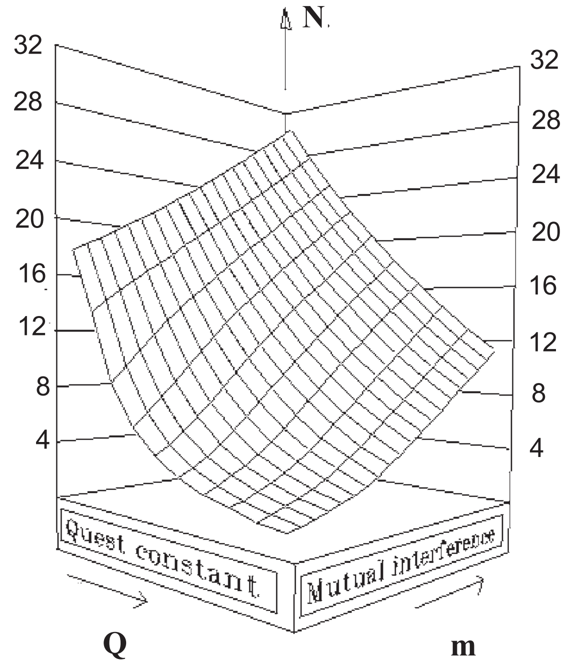


Fig.1. Probably steady-state density (N*) of gypsy moth population past introduction parasites

Рис. 1. Возможная точка динамического равновесия (устойчивая особая точка) популяции непарного шелкопряда после интродукции паразитоида.

Flareups of winter moth in Nova Scotia and British Columbia have occured at about 9- to 10-year intervals (although not neccessarily on oaks, and not at the high levels predicted [Roland, Embree, 1995].

The steady-state density of gypsy moth population (N^*) is important characteristic of gypsy moth population dynamics. Most likely it is close to the mean population density.

Analysis of the actual time-series showed that mean value of gypsy moth population density in the USA before application of classical biological control was about 58.0 eggmasses per 100 m^2.

It dropped down to approximately 3.9 eggmasses per 100 m^2 [Cambell, 1967] upon completing the first programmes on introduction. If we also take into account

Table 1. Predicted steady-state level of density of gypsy moth and its parasites population.
Таблица 1. Предсказанная точка динамического равновесия для популяции непарного шелкопряда и его паразитоидов

Companent of system	value of parametrs			
	mean Q_1, Q_2, m_1, m_2, R	Q_1+s, Q_2+s, m_1+s, m2+s, R	Q_1–s, Q_2–s, m_1–s, m_2–s, R	Q_1, Q_2, m_1, m_2, R+s
*L. dispar**	12.4	10.5	17.7	50.3
*Bl. scutelata***	36.7	19.9	123.2	123.0
*P. silvestris***	12.9	7.5	22.7	87.9

* Mean number of eggmasses per 100 m^2, ** Mean number of pupariaper 100 m^2.

data by Bess [1961] the value droppes down more, to about 1.6 (log10-scale)[1]. It is lower than threshold density that is recommended to switch on chemical control, 6 eggmasses per 100 m^2 , [Montgomery, 1990]. However, the problem of gypsy moth still remains partially due to inefficiency of the introduced parasites and predators [Price, 1990].

As it follows from our model analysis, introduction of two species of parasites (*Blepharipoda scutellata* and *Parasetigena silvestris*) may lead to stabilization of host population density. Its level (Fig. 1) is mainly higher than the threshold density recommended for switching on the control with chemicals. The predicted steady-state level of host population density is also much higher than the actual mean values. Partially it is caused by artificially low amount of parasitoid specied (2) used in the model. Actually, there are about 10 established parasitoids and predators [Clausen, 1956] affecting gypsy moth. We also have not paid any attention to the mammalian predators and birds.

We have not made any comparison of the data on the role of the above two parasitoids after introduction with the predicted one. The reason is that we were not able to find parallel long time series for the USA, characterizing *Blepharipoda*, *Parasetigena* and gypsy moth. There is no doubt that this data was collected many times, because many authors have published the analysis of these data [Burgess, Crossman, 1929; Bess, 1961; Campbell, 1967].

The applicability of the methodology described above will become finally clear by accomplishing the similar analysis with respect to other species. However, we think that is could be already accepted for preliminary evaluation of the results of introduction.

Of course, the accurate data on host and parasite population dynamics in the native area are needed to succeed.

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[1] An adequacy of the estimation of mean population density of insect is needed in additional research, which was not the task of this work.

Appendix 1. Population density dynamics.
Приложение 1. Динамика плотности популяции.

N1	N2	N0	Wbl	Wcc	Egg	Comments and reference
15.84	5.74	39.62	0.422	0.5	280.3	
5.74	4.36	15.84	0.594	0.233	172.0	
4.36	0.96	5.74	0.561	0.377	267.5	Znamenski and
0.96	0.10	4.36	0.526	0.416	286.4	Lyamtcev, 1990
0.10	0.15	0.96	0.150	0.399	230.1	Lyamtcev, 1985
0.15	0.23	0.10	0.125	0.520	370.0	
0.23	0.21	0.15	0.086	0.311	395.3	Panina, 1985
0.21	0.53	0.23	0.100	0.276	366.3	
0.53	3.29	0.21	0.1*	0.043	427.2	
3.29	6.96	0.53	0.12*	0.2*	390.3	
6.96	7.91	3.29	0.559	0.3*	398.4	
7.91	3.21	6.96	0.535	0.463	362.6	
40.00	33.50	15.00	0.030	0.001	300.0*	
33.50	16.00	40.00	0.330	0.630	314.0	
16.00	1.00	33.50	0.180	0.160	359.0	Yafaeva, 1963
1.00	1.50	16.00	0.001	0.020	309.0	
1.50	2.50	1.00	0.0003	0.001	221.0	
2.50	10.50	1.50	0.0003	0.001	396.0	
10.50	12.00	2.50	0.0001	0.220	380.0	
12.00	13.00	10.50	0.050	0.260	405.0	
13.00	22.50	12.00	0.080*	0.290	331.0	
5.30	341.90	0.30	0.049	0.009	350.0*	
341.90	248.10	5.30	0.122	0.013	350.0*	
248.10	2.90	341.90	0.260	0.017	350.0*	P. Sisojevic,
2.90	0.06	248.10	0.397	0.386	350.0*	1975
0.06	0.07	2.90	0.047	0.040	350.0*	

* Estimated values; density is given in number of individuals per 100 m^2; N1 — density of eggmass in spring of Nn-th year, N2 — density of egmass in spring of (Nn+1)-th year, N0 — density of eggmass in spring of (Nn–1)-th year, Wbl — proportion of population parasitised by *B. scutellata* in (Nn–1)-th year, Wcc — proportion of population parasitised by *P. silvestris* in (Nn–1)-th year, Egg — number of eggs in eggmass in fall of (Nn–2)-th year or in spring of (Nn–1)-th year.